A Survey of the Family Caprellidae (Crustacea, Amphipoda) from Selected Sites Along the Northern California Coast

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Abstract.—Nineteen species of caprellid amphipods representing six genera are described for the northern California coast. The study area extended from the Oregon-California border south to Fort Bragg. Twenty-one collecting sites were established and classified as to habitat type. The ranges for the following six species have been extended: *Caprella brevirostris*, *C. greenleyi*, *C. pustulata*, *C. alaskana*, *C. acanthogaster*, and *Cercops compactus*. The latter five species are new to California, and one of these, a new subspecies of *Caprella acanthogaster*, is described. A key is presented, and correlations between the types of coastal habitat and observed caprellid distribution patterns are discussed.

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The family Caprellidae was surveyed along the northern California coast between latitudes 39°N and 42°N. Nineteen species of caprellids are treated here. The ranges for six species have been extended, five of which have not been previously recorded from the California coast, thereby increasing the total number of species found on the California coast to twenty-four.

There are relatively few published accounts from the nineteenth century of caprellid amphipods occurring in the northeastern Pacific (Stimpson, 1857; Boeck, 1872; Mayer, 1882, 1890, 1903). Major investigations of the Caprellidae of the California coast during this century have been almost as limited. Dougherty and Steinberg (1953) published an account of the caprellids of California between latitudes 36°N and 38°N, although they made collections in only three localities, Dillon Beach, Moss Beach, and Monterey Bay. They described a new genus and two new species and recorded sixteen species previously described. They published a key to those species in Light et al. (1954).

Laubitz (1970) was the first since Mayer to reveal the diverse nature of the Caprellidae of the northeastern Pacific. She published an account of twenty-six species from the North American Pacific between latitudes 44°N and 60°N, including six new species and one new genus. In all, forty-one species of caprellids have been recorded from the Pacific Coast of North America prior to this work. Of these, twenty have been found along the California coast.

This paper discusses systematically all the species recorded, includes a key for their identification, and evaluates certain ecological factors which may affect the distribution of these organisms.

Materials and Methods

Specimens were collected from twenty-one selected sites between Fort Bragg, California, and the Oregon-California border between January 1971, and August

1972 (Figs. 1, 2). Collections were made at two locations at the Fort Bragg site (Point Cabrillo), one of which was subtidal and designated as Fort Bragg (1), and the other, intertidal, as Fort Bragg (2).

Intertidal collections were made during low tide periods. Samples of substrate suspected of housing caprellids were taken at each of the selected sites. These samples included bryozoans, hydroids, algae, sponges, ascidians, and asteroids. Some material was supplied by other collectors.

Subtidal specimens were obtained using scuba apparatus at Fort Bragg (1) and at an artificial reef in Humboldt Bay. An otter trawl, Smith-McIntyre bottom grab, and rock trawl were used to sample the nearshore benthos of Humboldt Bay. A complete reference collection of caprellids from this study has been deposited in the Invertebrate Museum, Department of Biology, Humboldt State University.

The recorded lengths for each species are of the largest male, the largest female, and the smallest ovigerous female.

An attempt was made to provide complete synonyms for each species, but where they became too lengthy, reference is made to an author which provides them in depth for that particular species.

Systematics

Family Caprellidae Dana, 1852

Diagnosis.—Head often partially fused with 1st segment of pereon; palp of maxilliped 1- to 4-jointed; pereon often with fewer than 7 pairs of legs, rarely 3 segments of pereon with brachial vescicles, 2 segments in female with marsupial plates, 1st joint of gnathopods and pereopods reduced; pleon and its legs rudimentary; eyes small, 1 pair; hepatopancreatic tubes 2, rectal glands none; heart with 3 pairs of ostia; posterior ganglia on nerve-chain very small, none situated in pleon (Laubitz, 1970).

Comments.—Mayer (1882, 1890, 1903) utilized eleven characters to differentiate genera within the Caprellidae. These were the number of articles in the flagellum of antenna 2, the number of articles in the mandibular palp and the setal formula for the terminal article, the presence or absence of swimming setae on antenna 2, the number of gill pairs, the number of appendage pairs on both the male and female abdomens, the number of articles in pereopods 3–5, and the length ratio of the inner and outer lobes of the maxilliped. McCain (1968) has since added to the list of generic characters the presence or absence of a molar and the position of the insertion of pereopod 5.

Laubitz (1970) has suggested that the setation of the female brood plates appears to be stable within each genus, and may serve as a generic character.

Several of Mayer's characters, such as the number of articles in pereopods 3–5 and the number of appendage pairs on both the male and female abdomens, appear to be quite unstable for the purpose of delineating caprellid genera. Both of these characters seem to be undergoing reduction, especially the abdomens, and therefore their continued use for delineating genera does not seem reliable.

The key below is based upon stable traits, and characteristics refer to both sexes unless otherwise stated. All tables used to compare species utilize adult male characteristics only.

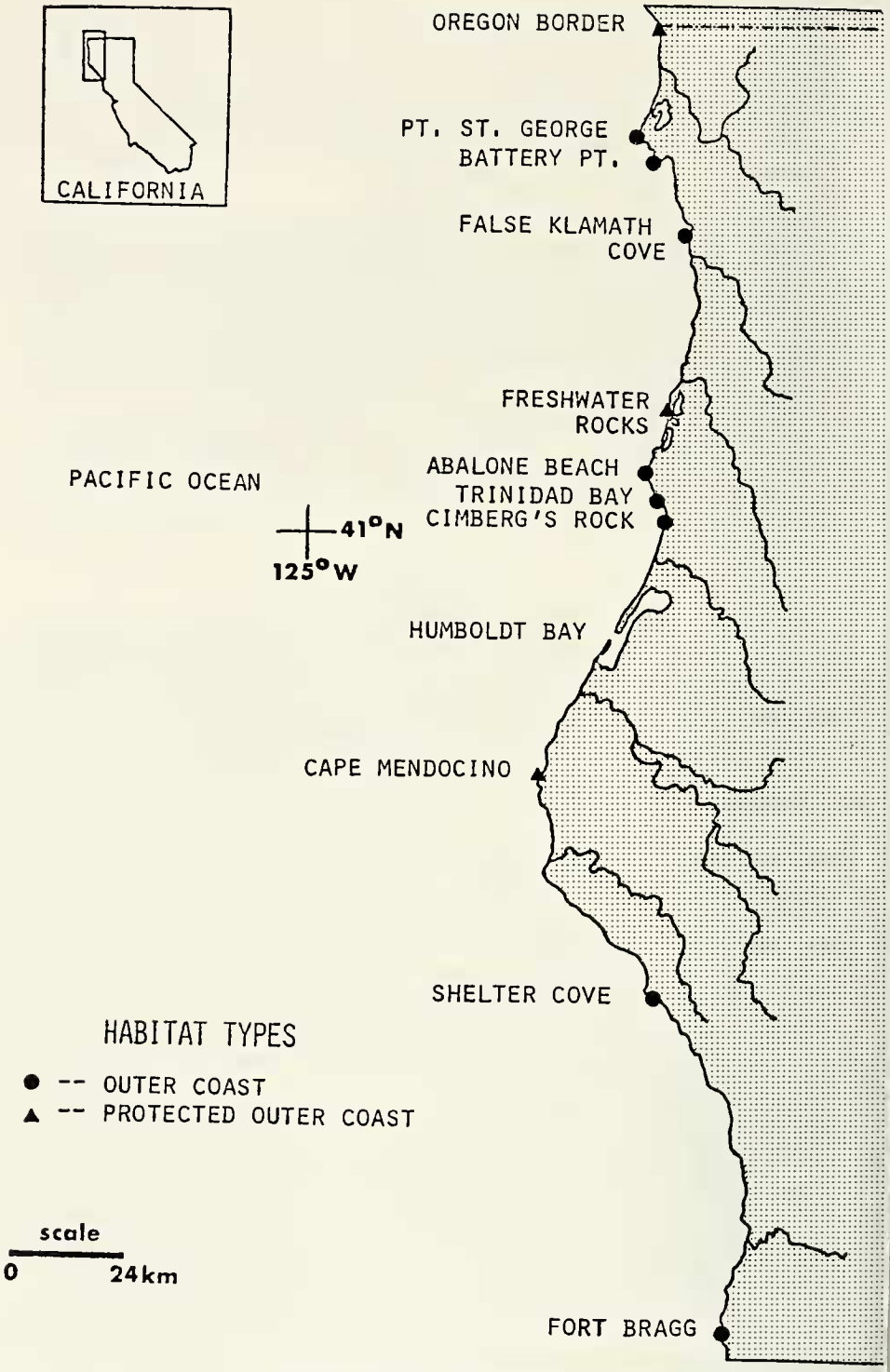

Fig. 1. Map of study area with collection sites indicated.

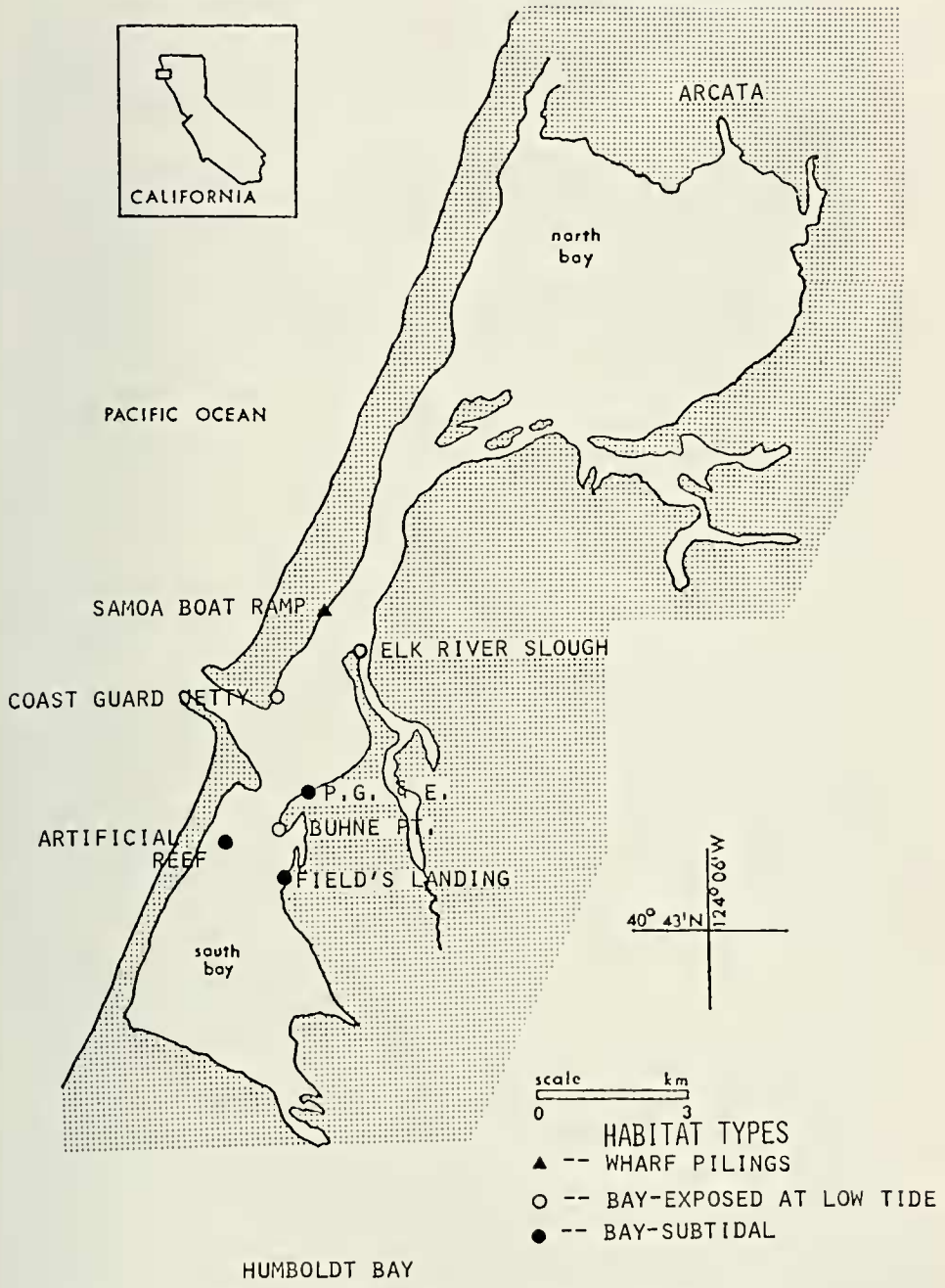

Fig. 2. Map of Humboldt Bay with collection sites indicated.

Key to the Caprellidae of the Northern California Coast

1A. Rudimentary pereopods present on pereonites 3 and 4; mandible with palp 2
1B. Rudimentary pereopods not present on pereonites 3 and 4; mandible without palp 6
2A. Gill pairs present on pereonites 3 and 4 3
2B. Gill pairs present on pereonites 2, 3, and 4 5
3A. Antenna 2 without swimming setae; cephalon with spine or knob ..... *Deutella californica*, p. 152
3B. Antenna 2 with swimming setae; cephalon smooth 4
4A. Pereonites 3 and 4 with median lateral projections over the gills; antenna 2 flagellum slender with long swimming setae; pereopods 5–7 articles slender ..... *Tritella pilimana*, p. 152
4B. Pereonites 3 and 4 without median lateral projections over the gills; antenna 2 flagellum stout with short setae; pereopods 5–7 articles stout ..... *Tritella laevis*, p. 152
5A. Abdomen five-segmented and with uropods; pereonites 5 and 6 short and stout ..... *Cercops compactus*, p. 151
5B. Abdomen minute; pereonites 5 and 6 long and slender ..... *Perotripus brevis*, p. 151
6A. Ventral spine present between insertions of gnathopods 2 7
6B. Ventral spine absent between insertions of gnathopods 2 9
7A. Cephalon with long, slender anteriorly directed projection; pereonite 5 with single median dorsal spine ..... *Caprella californica*, p. 158
7B. Cephalon flattened anteriorly and/or smooth; pereonite 5 without single median dorsal spine 8
8A. Pereonites 3–5 with antero-lateral projections . *Caprella equilibra*, p. 159
8B. Pereonites 3–5 without antero-lateral projections *Caprella mendax*, p. 162
9A. Palm of propodus of pereopods 5–7 straight or convex 10
9B. Palm of propodus of pereopods 5–7 concave 12
10A. Propodus of pereopods 5–7 with distinct tufts of long setae ..... *Caprella brevirostris*, p. 156
10B. Propodus of pereopods 5–7 without distinct tufts of long setae 11
11A. Propodus of gnathopod 2 massive, width two-thirds the length; antenna 1 flagellum uniarticulate ..... *Caprella greenleyi*, p. 159
11B. Propodus of gnathopod 2 length at least twice the width; antenna 1 flagellum with 16 articles in males and at least 18 articles in females ..... *Caprella alaskana*, p. 156
12A. Cephalon smooth or with paired spines or tubercles 13
12B. Cephalon with one spine or tubercle 16
13A. Pereon entirely smooth dorsally ..... *Caprella laeviuscula*, p. 162
13B. Pereon not entirely smooth dorsally 14
14A. Pereonite 5 with five pairs of spines dorsally ..... *Caprella acanthogaster humboldtiensis*, p. 154
14B. Pereonite 5 with three pairs of spines dorsally 15
15A. Pereonite 4 with paired spines postero-dorsally ... *Caprella ferrea*, p. 159
15B. Pereonite 4 with unpaired spines postero-dorsally ..... *Metacaprella kennerlyi*, p. 153

16A. Cephalon with dorsally directed single blunt projection ..... *Caprella pustulata*, p. 163
16B. Cephalon with anteriorly directed triangular projection 17
17A. Pleura absent; body spines never on pereonite 1 ..... *Caprella natalensis*, p. 163
17B. Pleura present; body spines always present on pereonite 1 18
18A. Pereon covered with large, blunt spines dorsally and laterally; antenna 1 flagellum with 9 articles in males and 7 articles in females ..... *Caprella verrucosa*, p. 164
18B. Pereon covered with small to medium-sized spines dorsally; antenna 1 flagellum with 11 articles in males and 9 articles in females ..... *Caprella incisa*, p. 161

Species Accounts

Genus *Cercops* Krøyer, 1842–43
Cercops compactus Laubitz, 1970

Cercops compactus Laubitz, 1970.

Material examined.—Battery Point, 1 female; False Klamath Cove, 2 males; Abalone Beach, 2 males; Shelter Cove, 1 male.

Remarks.—Four out of the six specimens of *C. compactus* examined possessed a small median dorsal tubercle on pereonite 6, and one specimen also possessed three very small tubercles on pereonite 5. The two specimens which lacked the tubercle on pereonite 6 were immature, measuring 1.6 mm; therefore the tubercle could be an adult characteristic. According to Laubitz (1970), her type specimens of *C. compactus* lack any kind of body spination. Until more specimens can be inspected, the significance of this variation in the spination of the posterior pereonites remains unclear.

Specimens were found on bryozoans, hydroids, and coralline algae. Length of largest male 3.0 mm and largest female 3.0 mm.

Distribution.—Type locality: Puffin Bay, Baranof Island, Alaska. Other localities: Cape Arago and Cape Blanco, Oregon.

Genus *Perotripus* Dougherty and Steinberg, 1953
Perotripus brevis (La Follette, 1915)

Paedaridium breve La Follette, 1915.
Perotripus brevis Dougherty and Steinberg, 1953, 1954; Laubitz, 1970.

Material examined.—Trinidad Bay, 1 female and 2 males.

Remarks.—Both Laubitz (1970) and I have found the outer lobe of maxilla 1 of *P. brevis* with four serrate spines instead of six as indicated by Dougherty and Steinberg (1953). Although the number of spines on maxilla 1 has been used as a taxonomic character, the reliability of this character is doubtful. Length of largest male 2.7 mm and largest female 2.2 mm.

Distribution.—Type locality: Laguna Beach, California. Other localities: Southern Prince William Sound, Alaska; Pacific coasts of Alexander Archipelago,

Alaska, and Vancouver Island, British Columbia; British Columbia mainland coast from Banks Island to Rivers Inlet; San Juan area, Washington.

Genus *Deutella* Mayer, 1890
Deutella californica Mayer, 1890

Deutella californica Mayer, 1890, 1903; Dougherty and Steinberg, 1953, 1954; Steinberg and Dougherty, 1957; Gardella, 1962; McCain, 1968; Laubitz, 1970.

Material examined.—Abalone Beach, 1 female; Trinidad Bay, 7 males, 4 females, and 1 juvenile; Samoa Boat Ramp, 7 males, 9 females, and 7 juveniles; Coast Guard Jetty, 4 males and 2 females; Elk River Slough, 16 males and 4 females; Humboldt Bay, 7 males and 7 females; Artificial Reef, 152 specimens; Fort Bragg (2), 1 female; Field's Landing, 39 males and 22 females.

Remarks.—Specimens were found on algae, bryozoans, hydroids, eelgrass, compound ascidians, and the tentacular radioles of the sabellid worm, *Eudistylia polymorpha*. Length of largest male 9.5 mm, largest female 6.0 mm, and smallest ovigerous female 2.5 mm.

Distribution.—Type locality: Cape Mendocino, California. Other localities: Southern Prince William Sound, Alaska; Juan de Fuca Strait, British Columbia; San Juan area, Washington; Pacific coasts of Vancouver Island, Washington and Oregon; "probably Port Aransas, Texas" (Steinberg and Dougherty, 1957); Monterey Bay and Mussel Point, California.

Genus *Tritella* Mayer, 1890
Tritella laevis Mayer, 1903

Tritella laevis Mayer, 1903; Dougherty and Steinberg, 1953, 1954; McCain, 1968; Laubitz, 1970.

Material examined.—Point Saint George, 4 males, 4 females, and 1 juvenile; Battery Point, 14 males, 2 females, and 53 juveniles; Abalone Beach, 4 males, 3 females, 26 juveniles; Shelter Cove, 3 males, 6 females, and 4 juveniles; Fort Bragg (2), 3 males, 4 females, and 2 juveniles.

Remarks.—Specimens were found on hydroids, algae, bryozoans, coralline algae, and sponges. Length of largest male 6.5 mm, largest female 5.7 mm, and smallest ovigerous female 3.2 mm.

Distribution.—Type locality: Santa Catalina Island, California. Other localities: Mainland coast of Queen Charlotte Sound and Queen Charlotte Strait, British Columbia; Washington and British Columbia coasts of Juan de Fuca Strait; Pacific coasts of Queen Charlotte Islands, Vancouver Island and Oregon; Pacific Grove, Dillon Beach, Moss Beach and Monterey Bay, California.

Tritella pilimana Mayer, 1890

Tritella pilimana Mayer, 1890, 1903; Dougherty and Steinberg, 1953, 1954; McCain, 1968; Laubitz, 1970.
Aeginella hirsuta La Follette, 1915.

Material examined.—Oregon Border, 190 males, 136 females, and 95 juveniles; False Klamath Cove, 2 males, 1 female, and 7 juveniles; Freshwater Rocks, 10 males and 9 females; Trinidad Bay, 30 males, 31 females, and 17 juveniles; Cim-

berg's Rock, 2 males and 1 female; Samoa Boat Ramp, 24 males, 17 females, and 16 juveniles; Coast Guard Jetty, 4 males and 1 female; Elk River Slough, 4 males, 1 female, and 6 juveniles; Cape Mendocino, 1 male; Field's Landing, 1 male and 1 female; Humboldt Bay, 6 males, and 15 females; Artificial Reef, 1,094 specimens.

Remarks.—One 'female' intersex specimen of *Tritella pilimana* was found among the 1,094 specimens collected from the Artificial Reef in South Humboldt Bay. This intersex specimen possessed male gnathopod 2, an abdomen with penes, female brood plates, and genital openings on the posterior ventral surface of pereonite 5.

The published accounts of caprellid intersexes are limited. Mayer (1903) made record of two "Hermaphite" specimens of *Caprella bispinosa* Mayer (1890). Laubitz (1970) reported two intersex specimens of *Tritella laevis* Mayer (1903) and Laubitz and Mills (1972) have noted that all the type specimens of *Thorina spinosa* Stephensen (1944) were intersexes. Laubitz (1972) also found intersex specimens of *Aeginia longicornis* Krøyer, 1842–43 and recently noted (Laubitz, pers. comm.) intersexes in one species of *Dulichia* (Gammaridea; Podoceridae). Kevin C. Myers (pers. comm.) of San Francisco State University has reported intersexes of *Caprella equilibra* Say (1818) collected in San Francisco Bay. I have also found intersexes in *Caprella incisa* Mayer (1903) and *Caprella laeviuscula* Mayer (1903) which are discussed below.

Specimens were found on hydroids, bryozoans, coralline algae, algae, eelgrass, compound ascidians, and the tubes of sabellid worms. Length of largest male 8.3 mm, largest female 5.2 mm, and smallest ovigerous female 3.0 mm.

Distribution.—Type locality: Mendocino, California. Other localities: Southern Prince William Sound, Alaska; Dixon Entrance and mainland coast south to Johnstone Passage, British Columbia; Washington coast of Juan de Fuca Strait; San Juan area, Washington; Pacific coasts of Queen Charlotte Islands, Vancouver Island and Oregon; Humboldt Bay, Laguna Beach, Dillon Beach, and Moss Beach, California.

Genus *Metacaprella* Mayer, 1903

Metacaprella kennerlyi (Stimpson, 1864)

Caprella kennerlyi Stimpson, 1864; Mayer, 1882, 1903; Holmes, 1904; Johnson and Snook, 1927; Wailes, 1931; Light, 1941; Ricketts and Calvin, 1952.

Metacaprella kennerlyi Dougherty and Steinberg, 1953, 1954; Gardella, 1962; Saunders, 1966; Laubitz, 1970.

Material examined.—Freshwater Rocks, 2 females; Trinidad Bay, 8 males and 5 females; Cimberg's Rock, 2 males and 1 female; Samoa Boat Ramp, 1 female; Artificial Reef, 1 specimen; Fort Bragg (1), 2 males and 7 females; Nearshore Benthos off Humboldt Bay, 42 males and 34 females.

Remarks.—Specimens were found on hydroids, bryozoans, the exterior shell surface of an abalone, and the tentacular radioles of the sabellid worm, *Eudistylia polymorpha*. Length of largest male 22.0 mm, largest female 9.0 mm, and smallest ovigerous female 7.0 mm.

Distribution.—Type locality: Puget Sound, Washington. Other localities: Popof Bay, Yadutat, Dutch Harbour and Kodiak Harbour, Alaska; Washington and British Columbia coasts of Strait of Georgia and Juan de Fuca Strait; Pacific

coasts of British Columbia, Vancouver Island, Washington and Oregon; Queen Charlotte Islands; off Washington and Oregon; Friday Harbor, Washington; California coast south to Santa Barbara.

Genus *Caprella* Lamarck, 1801

Caprella acanthogaster humboldtiensis, new subspecies

Figure 3

Material examined.—Field's Landing, 71 males and 55 females; holotype and paratypes deposited in the Invertebrate Museum, Department of Biology, Humboldt State University, Arcata, California; paratypes deposited in the National Museum of Natural Science in Canada, Ottawa, Canada.

Description.—Body spination of male as follows: Cephalon and pereonite 1 smooth dorsally, pereonite 2 with one to three pairs of small spines posteriorly, pereonite 3 with seven spine pairs along its length, pereonite 4 with eight pairs along its length, pereonite 5 with five spine pairs, pereonites 6 and 7 with paired spines medially and posteriorly; laterally, spines at the base of second gnathopod, posterior spines on pereonite 2, seven spines marginally on pereonites 3 and 4, and two spines anteriorly on pereonite 5. Cephalon, pereonites 1 and 2, and gnathopod 2 set with long setae, quite dense in older males; males also exhibit elongation of pereonites 1 and 2. In females, cephalon usually smooth but may have one pair of spines, pereonite 1 always bearing one pair of spines postero-dorsally pereonites 2–5 with variable spination both laterally and dorsally, pereonites 6 and 7 similar to that of the male; in both sexes, occasional unpaired spines dorsally or laterally on the pereon; pleura slightly developed. Length of largest male found 18.0 mm, largest female 11.0 mm, and smallest ovigerous female 6.0 mm.

Antenna 1 of male almost as long as cephalon plus pereonites 1–3, female antenna 1 longer than cephalon plus pereonites 1–4, flagellum with twenty-five articles in males and nineteen articles in females. Peduncle article 3 of antenna 1 produced into a small projection antero-dorsally. Antenna 2 shorter than the two basal articles of antenna 1 in males; in females, antenna 2 shorter than peduncle articles 1–3 of antenna 1, flagellum with swimming setae.

Mouthparts typical of genus; lacinia mobilis of right mandible denticulate but not five-toothed.

Propodus of gnathopod 1 with 2 proximal grasping spines, grasping margin of dactylus and propodus serrate. In males, gnathopod 2 propodus almost three times as long as wide, and only slightly longer than basis, palm with large projection proximo-medially with grasping spine, also poison tooth between proximo-medial projection and a distal triangular projection; dactylus heavy and scimitar-shaped; basis having an antero-lateral projection distally, and attached posteriorly on pereonite 2. Female gnathopod 2 propodus longer than basis, palm with proximal grasping spine and two accessory spines, distal minute poison tooth and more distal rounded projection, basis attached anteriorly on pereonite 2.

Gills ovate to elliptical in both sexes.

Pereopods 5–7 increasing in length posteriorly, propodus with 2 proximo-medial grasping spines, palm expanded near grasping spines.

Abdomen of male and female typical of genus.

Brood plates of female typical of genus.

Remarks.—*Caprella acanthogaster* Mayer (1890) was originally described from

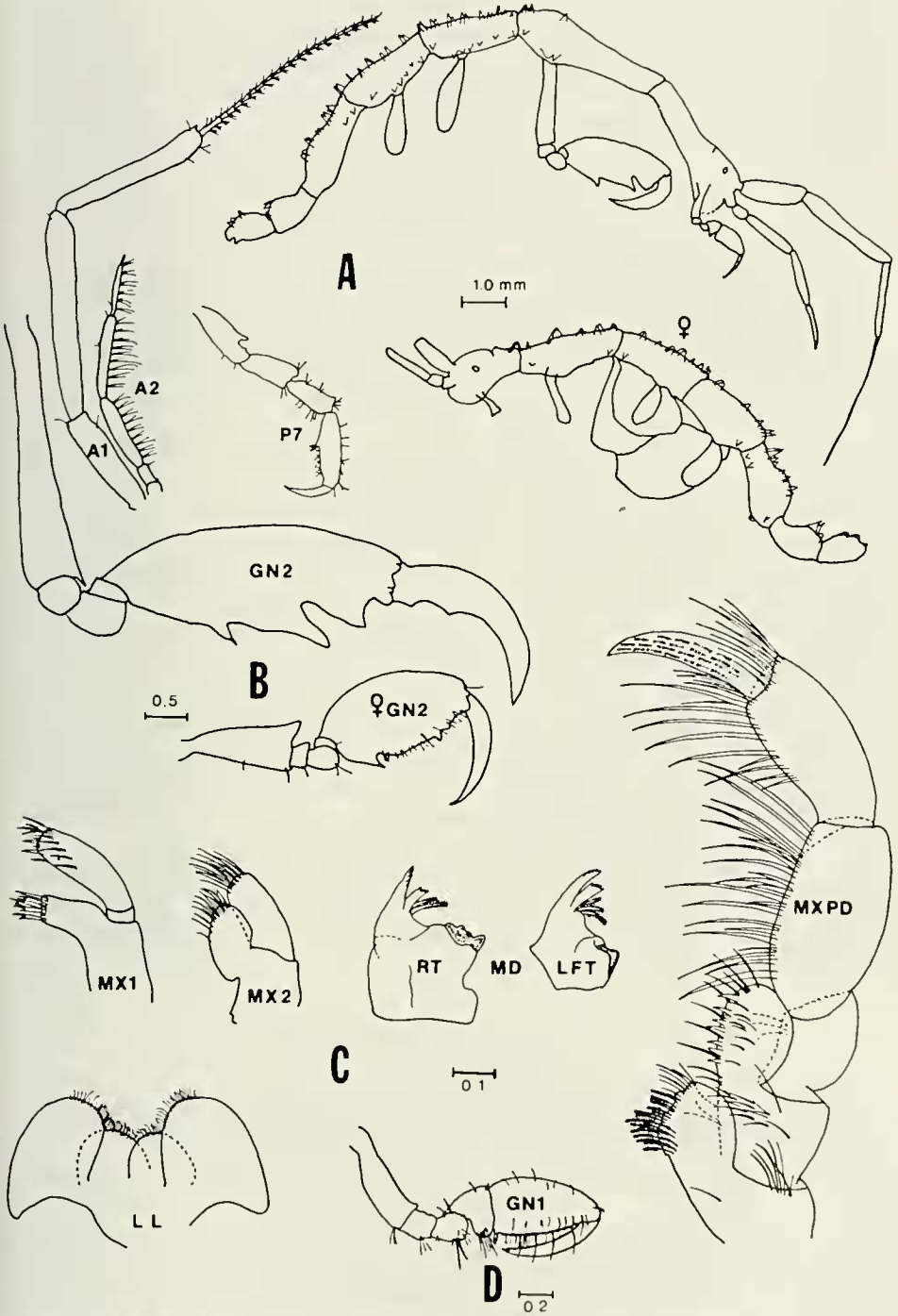

Fig. 3. *Caprella acanthogaster humboldtiensis*: A. Male and female, lateral view; appendages, antenna 1, antenna 2, and pereopod 7; B. Male gnathopod 2 and female gnathopod 2; C. Male mouthparts; D. Male gnathopod 1; measurements are in millimeters. Key to figure symbols: A = antenna; GN = gnathopod; LFT = left; LL = lower lip; MD = mandible; MX = maxilla; MXPD = maxilliped; P = pereopod; and RT = right.

along the coast of China, and from that description and the description in Mayer's (1903) monograph there appear to be certain differences between the species he described and my specimens (Table 1). These morphological distinctions plus the geographical distance between the populations are my basis for assigning the specimens to a new subspecies.

Specimens of *C. acanthogaster humboldtiensis* were found on the hydroids *Obelia borealis* and *Plumularia corrugata*. One specimen of *C. acanthogaster humboldtiensis* was observed with a polyp of the hydroid *Obelia* sp. attached to the dorsal surface of pereonite 2.

Caprella acanthogaster humboldtiensis at Field's Landing in Humboldt Bay comprised forty percent of the caprellid collection at that location and was associated with five other species of caprellids common to the Bay. It is suspected that this species was introduced into the Bay by the fouling on ships or with oyster spat *Crassostrea gigas* which were imported from Japan.

Caprella alaskana Mayer, 1903

Caprella alaskana Mayer, 1903; Laubitz, 1970.

Material examined.—Trinidad Bay, 2 males; Samoa Boat Ramp, 1 female.

Remarks.—This species shows great variation in the degree of spination on the cephalon and pereon. Specimens described by Mayer (1903) were quite spiny in comparison to those examined by Laubitz (1970), which were almost spineless. According to Laubitz (1970), "The differences are, in fact, so great that they create a doubt that these are members of the same species." Laubitz (pers. comm.) has since emphasized that, in species where the body spination is highly variable, this character is not reliable. The specimens found within my study area were moderately spiny, and the spination of males and female was quite similar.

Specimens were found on bryozoans and the tubes of sabellid worms. Length of largest male 9.2 mm and largest female 8.5 mm.

Distribution.—Type locality: Not known, probably Alaska. Other localities: Aleutian Islands, Kodiak Island, Prince William Sound, and Alexander Archipelago, Alaska; Fort Rupert, Queen Charlotte Islands, Queen Charlotte Strait, and Vancouver Island, British Columbia.

Caprella brevirostris Mayer, 1903
Figure 4

Caprella brevirostris Mayer, 1903; Dougherty and Steinberg, 1953, 1954.
Caprella septentrionalis La Follette, 1914 (*non* Krøyer, 1842–43.)

Material examined.—Fort Bragg (1), 1 male; Fort Bragg (2), 5 males and 5 females.

Description.—Cephalon with small anteriorly directed triangular projection, pereonites 1–5 smooth, pereonite 6 with paired spines postero-laterally, pereonite 7 with paired spines postero-laterally and one postero-medial spine; pereonites 1 and 2 are elongated in males with posterior pereonites shortening quickly.

Antenna 1 in males longer than cephalon plus pereonites 1 + 2; in females, antenna 1 longer than cephalon plus pereonites 1–3; flagellum with twelve articles in males and eight articles in females. Antenna 2 of male as long as peduncle

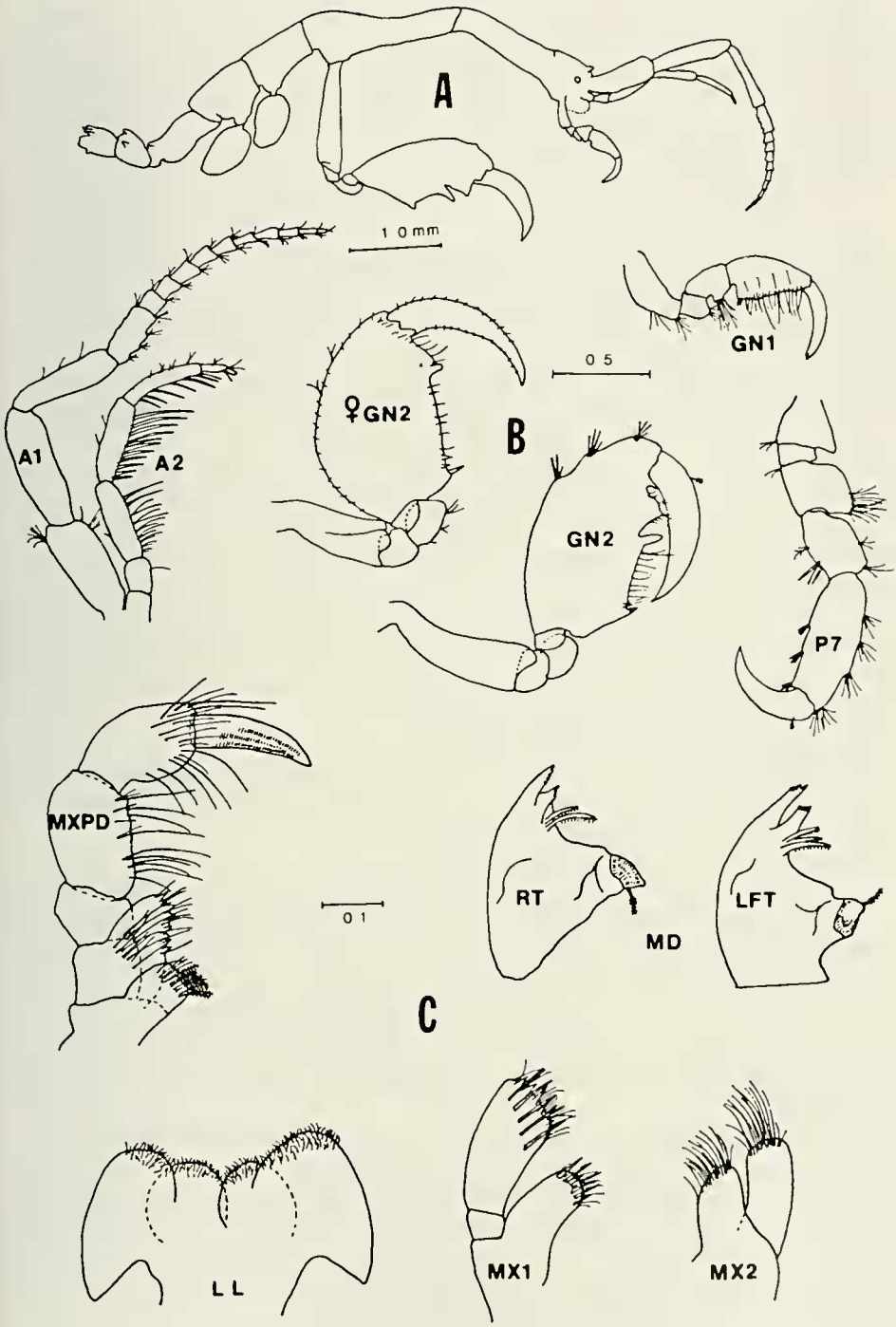

Fig. 4. *Caprella brevirostris*: A. Male, lateral view; B. Female gnathopod 2; and male antenna 1, antenna 2, gnathopod 1, gnathopod 2, and pereopod 7; C. Male mouthparts; measurements are in millimeters. Symbols as in Figure 3.

Table 1. Morphological distinctions between *Caprella acanthogaster acanthogaster* and *C. a. humboldtiensis*.

	C. a. acanthogaster	*C. a. humboldtiensis*
Size (largest)	42 mm	18 mm
Gills	long, slender	ovate to elliptical
Spination of pereonite 5	approximately 10 pairs of spines	5 pairs of spines

articles 1 + 2 of antenna 1; in females, antenna 2 longer than entire peduncle of antenna 1, flagellum with swimming setae.

Mouthparts typical of genus; lacinia mobilis of right mandible toothed but not five-toothed.

Propodus of gnathopod 1 with 2 proximal grasping spines, grasping margin of dactylus and propodus serrate. Gnathopod 2 propodus of males almost twice as long as broad, and with tufts of setae antero-dorsally and on the sides of palmar projections, palm with proximo-medial projection with grasping spine and accessory spine, palm also with distal acute poison tooth and more distal triangular projection; dactylus somewhat scimitar-shaped with serrate grasping margin; ischium with antero-lateral rounded projection; basis curved at distal end, attached posteriorly on pereonite 2, and having two small antero-dorsal ridges. Female gnathopod 2 propodus longer than basis, palm with proximal grasping spine and two accessory spines, also small acute poison tooth distally and more distal rounded projection; basis attached anteriorly on pereonite 2, and having antero-distal ridge with terminal rounded projection.

Gills oval to oblong in males and females.

Pereopods 5–7 increasing in length posteriorly, propodus with three tufts of truncated spines on palm, convex surface with tufts of long setae.

Abdomen in both sexes typical of genus.

Brood plates of female typical of genus.

Remarks.—In his 1903 monograph, Mayer devoted one paragraph and four figures to the actual description of *C. brevirostris*. Since that time subsequent authors have given mere mention of this species, therefore, I have given a complete redescription and set of figures.

My specimens varied from Mayer's (1903) descriptions only in size. His largest male and female specimens measured 12.0 mm and 5.0 mm, respectively, whereas my largest male measured 7.5 mm and the largest and smallest ovigerous female measured 3.0 mm.

Specimens were found on a hydroid, an alga, and the exterior shell surface of an abalone.

Distribution.—Type locality: Straits of Korea. Other localities: Pacific coasts of Korea and China; Pacific Grove and Tomales Point, California.

Caprella californica Stimpson, 1857

Refer to Laubitz (1970); *see also* Keith, 1969, 1971.

Material examined.—Abalone Beach, 1 female; Trinidad Bay, 1 male and 1 female; Samoa Boat Ramp, 4 males, 4 females, and 1 juvenile; Elk River Slough, 2 males and 1 female; Artificial Reef, 436 specimens; Field's Landing, 55 males and 56 females; Humboldt Bay, 19 males and 25 females.

Remarks.—Mayer (1903) separated the three varieties of *Caprella scaura* on the basis of the spination of pereonite 5. Laubitz (1970) assigned two of the varieties, *spinorostris* and *scauroides*, to the third, *C. californica*, because of the high degree of variability in body spination seen in *C. californica*. Considering the variations seen in my specimens, Laubitz' decision appears justified.

Specimens were found on algae, eelgrass, hydroids, and the tubes of sabellid worms. Length of largest male 19.5 mm, largest female 14.1 mm, and smallest ovigerous female 6.5 mm.

Distribution.—Type locality: San Francisco Bay, California. Other localities: South China Sea and Formosa Strait; Korea Strait and off Korea; Tsugaru Strait and off southwestern Japan; Queen Charlotte Islands, Hecate Strait, Queen Charlotte Sound, and Strait of Georgia, British Columbia; Pacific coasts of Vancouver Island and Washington; Juan de Fuca Strait and San Juan area, Washington; California from San Diego to Humboldt Bay; Caldera, Chile.

Caprella equilibra Say, 1818

Refer to McCain, 1968; *see also* Light, 1941; Laubitz, 1970; Keith, 1969, 1971.

Material examined.—Field's Landing, 1 female; Pacific Gas and Electric Company Nuclear Power Plant Outflow Canal, 19 males and 23 females; Artificial Reef, 257 specimens.

Remarks.—Specimens were found on hydroids and bryozoans. Length of largest male 15.0 mm, largest female 7.0 mm, and smallest ovigerous female 5.0 mm.

Distribution.—Type locality: South Carolina. Other localities: *See* McCain, 1968; also San Juan area, Washington; Vancouver Island, Queen Charlotte Sound, and Hecate Strait, British Columbia.

Caprella ferrea Mayer, 1903

Caprella ferrea Mayer, 1903; Laubitz, 1970.
Metacaprella ferrea Dougherty and Steinberg, 1953, 1954.

Material examined.—Freshwater Rocks, 3 males and 4 females; Trinidad Bay, 22 males and 20 females; Samoa Boat Ramp, 2 males and 3 females; Fort Bragg (1), 1 male; Fort Bragg (2), 1 female.

Remarks.—Specimens of *C. ferrea* collected at Freshwater Rocks differed from Laubitz' (1970) description in that peduncular segments 2 and 3 of antenna 1 were heavily setose.

Specimens were found on hydroids, bryozoans, the tubes of sabellid worms, and the exterior shell surface of an abalone. Length of largest male 9.0 mm, largest female 6.5 mm, and smallest ovigerous female 4.5 mm.

Distribution.—Type locality: Humboldt Bay, California. Other localities: Moss Beach and Monterey Bay, California; Pacific coasts of Vancouver Island and Queen Charlotte Islands, British Columbia; Alexander Archipelago, Alaska.

Caprella greenleyi McCain, 1969
Figure 5

Caprella greenleyi McCain, 1969.

Material examined.—Abalone Beach, 2 males; Cimberg's Rock, 1 female.

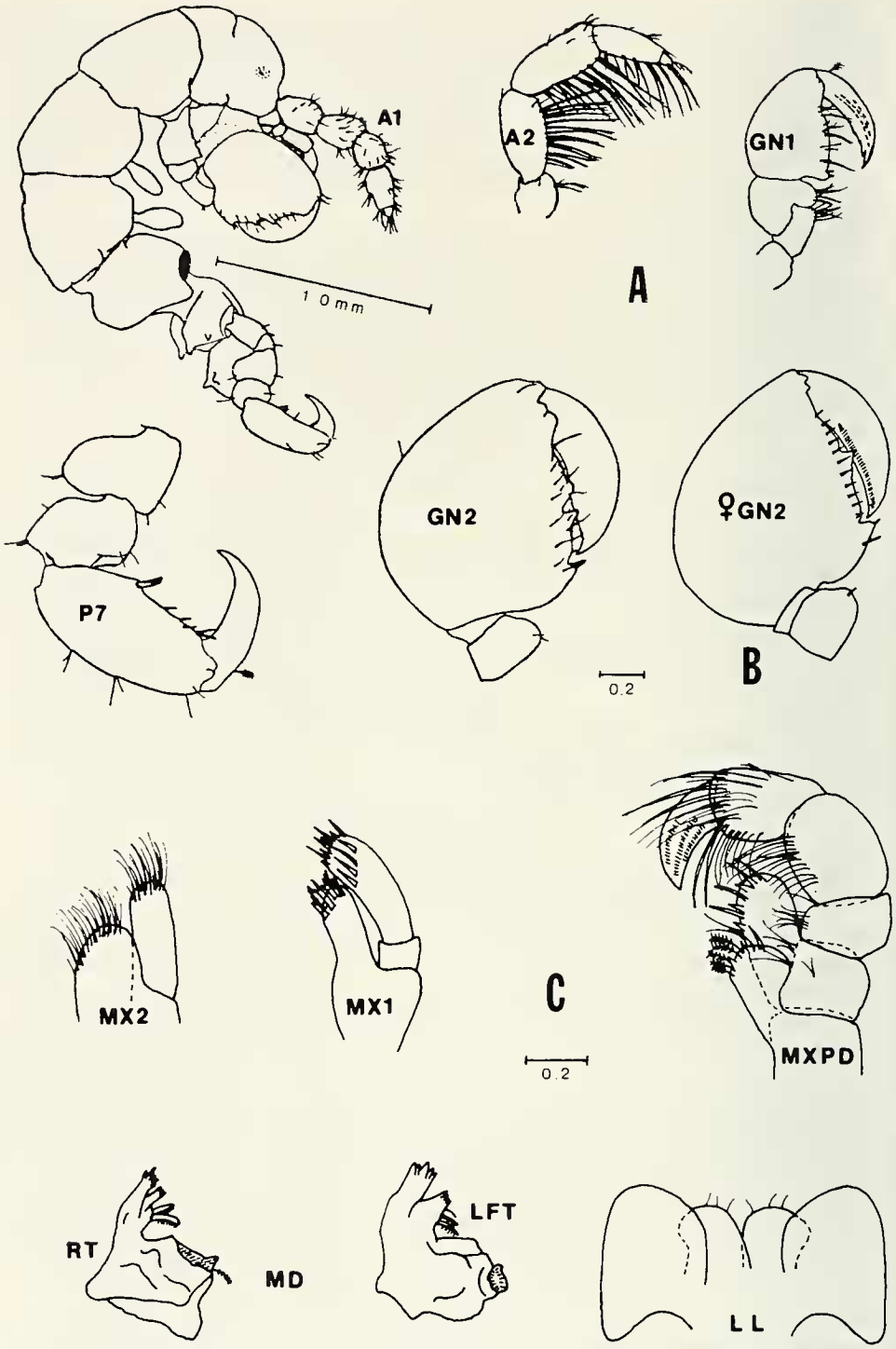

Fig. 5. *Caprella greenleyi*. A. Male, lateral view, antenna 1, antenna 2, gnathopod 1, gnathopod 2, and pereopod 7, not to scale (from McCain, 1969); B. Female gnathopod 2; C. Female mouthparts; measurements are in millimeters. Symbols as in Figure 3.

Description.—Cephalon, body, and appendages robust and covered with microtubercles, small median dorsal paired tubercles on pereonite 5, large median dorsal paired tubercles on pereonites 6 and 7, anteriorly directed pleural projections on pereonites 3 and 4.

Antenna 1 approximately equal to pereonites 1 + 2, flagellum uniarticulate. Antenna 2 shorter than antenna 1, flagellum uniarticulate, with swimming setae.

Mouthparts typical of genus; lacinia mobilis of right mandible toothed but not five-toothed.

Propodus of gnathopod 1 with 2 proximal grasping spines, grasping margin of dactylus and propodus serrate. In males, propodus of gnathopod 2 approximately two-thirds as broad as long, palm with 2 proximal grasping spines and medial notch; in females, propodus of gnathopod 2 palm with single medial projection; dactylus in both sexes massive and scimitar-shaped with slightly serrate grasping margin; basis attached medially on pereonite 2 in males and females and having antero-lateral ridge.

Gills oval in males and females.

Pereopods 5–7 stout, slightly increasing in length posteriorly, propodus with 2 proximal grasping spines.

Abdomen of both sexes typical of genus.

Remarks.—*Caprella greenleyi* is an unusually small caprellid species, the original description was based on specimens ranging from 2.7 mm to 3.6 mm. My recorded lengths were: largest male 1.5 mm, largest female 2.3 mm, and no ovigerous female was found. This species was first found clinging to the sea star *Henrica leviscula* (Stimpson, 1857); McCain (1968) suspected it of having a direct association with that particular sea star. Inspection of over 300 specimens of *H. leviscula* in this study failed to produce any specimens of *Caprella greenleyi*.

My specimens of *C. greenleyi* possess enough variation from the original description (McCain, 1968) to warrant the supplemental redescription and figures which are presented.

Specimens were found on a coralline alga and bryozoans.

Distribution.—Type locality: Boiler Bay, Oregon. New records: Abalone Beach and Cimberg's Rock, California.

Caprella incisa Mayer 1903

Caprella acutifrons var. *incisa* Mayer 1903.

Caprella incisa Dougherty and Steinberg 1953, 1954; McCain 1968; Laubitz 1970.

Material examined.—Point Saint George, 5 males and 1 female; Battery Point, 18 males and 13 females; False Klamath Cove, 1 male; Trinidad Bay, 3 males and 3 females; Buhne Point, 35 males and 42 females; Artificial Reef, 14 specimens; Fort Bragg (1), 3 males; Fort Bragg (2), 178 males, 209 females, and 1 intersex.

Remarks.—Specimens of *C. incisa* examined in this study included two distinct size classes and one intersex specimen. Adult specimens found north of Trinidad Bay were unusually small (approximately 5.0 mm), but I have included them with *C. incisa* on the basis of the type of spination, some pleural development, distal palmar development on gnathopod 2, and general body proportions. The adult specimens found south of Trinidad Bay were of 'normal' size.

The so-called 'female' intersex specimen of *Caprella incisa* possessed male gnathopod 2 and abdomen with penes, and female brood plates and genital openings on the posterior ventral surface of pereonite 5.

Specimens were found on hydroids, bryozoans, coralline algae, and algae. Length of largest male 11.0 mm, largest female 7.5 mm, and smallest ovigerous female 3.0 mm.

Distribution.—Type locality: California, precise locality not known. Other localities: Pacific coasts of Oregon, Washington, Vancouver Island, and Alexander Archipelago; Washington coast of Juan de Fuca Strait; Queen Charlotte Sound, British Columbia; Pacific Grove, Santa Catalina Island, Point Reyes, Dillon Beach, and Moss Beach, California.

Caprella laeviuscula Mayer, 1903

Refer to Laubitz, 1970.

Material examined.—Abalone Beach, 2 males and 3 females; Trinidad Bay, 118 males, 42 females, and 23 juveniles; Samoa Boat Ramp, 21 males, 31 females, and 12 juveniles; Elk River Slough, 2 males; Artificial Reef, 1,825 specimens; Field's Landing, 4 males and 12 females; Humboldt Bay, 297 males, 493 females, and 440 juveniles.

Remarks.—The 1,825 individuals of *C. laeviuscula* collected from the Artificial Reef included five intersex specimens. Four of these specimens possessed male second gnathopods, penes, female brood plates, and female genital openings on the posterior ventral surface of pereonite 5. The fifth specimen possessed only secondary sex characteristics of both sexes and male genitalia; there was no sign of female genitalia on pereonite 5 of this specimen.

Several individuals of *C. laeviuscula* were inspected which had the epiphytic diatom *Isthmia nervosa* attached to the dorsal surface of the pereon. Caprellids are often found covered with detritus, but rarely with living material. On one occasion prior to the initiation of this study, I found large numbers of the hydroid *Clytia* sp. attached to the dorsal surface of the pereon of several active, apparently healthy caprellids. The presence of detritus or living material may serve as camouflage.

Specimens were found on hydroids, bryozoans, compound ascidians, alga, eelgrass, and the tubes of sabellid worms. Length of largest male 15.2 mm, largest female 7.0 mm, and smallest ovigerous female 3.0 mm.

Distribution.—Type locality: Pacific coast of North America, precise locality not known. Other localities: Akkesni Bay, Japan; Kodiak, Adakh, Prince William Sound, and Alexander Archipelago, Alaska; Queen Charlotte Islands, Queen Charlotte Sound, Queen Charlotte Strait, Strait of Georgia, Juan de Fuca Strait, Victoria Harbor, and Fort Rupert, Vancouver Island, and the Pacific Coast of Vancouver Island, British Columbia; Puget Sound, Washington; Pacific coast of Oregon; Humboldt Bay and (?) Monterey Bay, California.

Caprella mendax Mayer, 1903

Caprella mendax Mayer, 1903; Laubitz, 1970.
Caprella equilibra Dougherty and Steinberg, 1953.

Material examined.—Benthos off Humboldt Bay, 1 female, 7.9 mm.

Table 2. Comparison of morphological characteristics between *Caprella scabra*, *C. pustulata* and *C. pilipalma*.

	C. scabra	*C. pustulata*	*C. pilipalma*
Cephalic spine	pointed, stout	blunt, stout	pointed, slim
Antenna 1 length	scarcely ⅓ body length	⅓ body length	⅓ body length
setation	none	dense	none
Gnathopod 2 attachment	median	posterior	posterior to median
poison tooth	present	present	absent
setation	none	dense	dense
grasping spine	none	one, small proximal	none
Spination (body)	small, low anteriorly; larger posteriorly	raised and large	low and small

Remarks.—The single specimen was collected in a Smith-McIntyre bottom grab at a depth of 80 meters off Humboldt Bay.

Distribution.—Type locality: California, precise locality not known. Other localities: Pacific Grove, Santa Barbara, and San Diego, California; Vancouver Island and Hecate Strait, British Columbia; San Juan Islands, Washington.

Caprella natalensis Mayer, 1903

Refer to Laubitz, 1972.

Material examined.—Battery Point, 3 males and 1 female; Trinidad Bay, 1 male; Cimberg's Rock, 3 males and 3 juveniles; Buhne Point, 16 males and 39 females; Humboldt Bay, 13 females; Fort Bragg (1), 4 males and 7 females; Fort Bragg (2), 13 males and 15 females.

Remarks.—Laubitz (1972) presented an excellent discussion of a portion of the *Caprella acutifrons* group, in which she gave *C. acutifrons* var. *natalensis* specific status. McCain (1968) has presented a thorough treatment of the group as a whole and also discussed the current taxonomic standing of the remaining varieties.

Specimens were found on bryozoans, hydroids, algae, and the exterior shell surface of an abalone. Length of largest male 9.6 mm, largest female 7.5 mm, and smallest ovigerous female 4.0 mm.

Distribution.—Type locality: Port Natal, Indian Ocean. Other localities: Durban, Cape Town, and Cape Peninsula, South Africa; South West Africa; Tristan da Cunha; Queen Charlotte Islands, British Columbia south to Oregon; Pacific Grove and Santa Cruz, California.

Caprella pustulata Laubitz, 1970

Caprella pustulata Laubitz, 1970.

Material examined.—Oregon border, 5 males, 1 female, and 13 juveniles; Freshwater Rocks, 3 males and 3 females; Abalone Beach, 3 males and 1 female; Samoa Boat Ramp, 1 male; Elk River Slough, 2 males and 3 females.

Remarks.—Those adult specimens of *C. pustulata* collected in the northern portion of the study area were unusually small (approximately 4.0 mm). The occurrence of these small-sized adults in this species and *C. incisa* suggests that the populations sampled were young at the time of collection (winter), or their adult size is limited by some environmental factor.

Since *C. pustulata* is quite similar in structure and distribution to *C. scabra* Holmes (1904) and *C. pilipalma* Dougherty and Steinberg (1953), Table 2 is made from the original descriptions for reference.

Specimens were found on hydroids, bryozoans, and the tubes of sabellid worms. Length of largest male 9.0 mm, largest female 4.5 mm, and smallest ovigerous female 3.5 mm.

Distribution.—Type locality: Gudal Bay, Graham Island, Queen Charlotte Islands, British Columbia. Other localities: Baranof Island, Prince William Sound, and Canoe Bay, Alaska; Vancouver Island, Koeye Estuary, and Queen Charlotte Islands, British Columbia; Washington and Oregon.

Caprella verrucosa Boeck, 1872

Refer to Laubitz, 1970.

Material examined.—Point Saint George, 1 male; Battery Point, 1 male and 3 females; False Klamath Cove, 2 males, 1 female, and 2 juveniles; Trinidad Bay, 1 female and 2 juveniles; Fort Bragg (2), 2 males, 1 female, and 1 juvenile; Cimberg's Rock, 15 males, 10 females, and 4 juveniles.

Remarks.—Specimens were found on hydroids, bryozoans, and coralline algae. Length of largest male 5.5 mm, largest female 4.5 mm, and smallest ovigerous female 2.7 mm.

Distribution.—Type locality: California, probably near San Francisco. Other localities: Misaki, Yokohama. Tateyama Bay, and Onagawa Bay, Japan; Pacific coasts of Queen Charlotte Islands, Vancouver Island and Washington; Dillon Beach, Pacific Grove, Santa Catalina Island, Point Reyes, and Laguna Beach, California.

Discussion

Nineteen species of caprellid amphipods representing six genera were found in this study. Five other species have been recorded previously from the California coast: *Tritella tenuissima*, *Caprella gracilior*, *C. uniforma*, *C. pilipalma*, and *Metacaprella anomala*. The first two are typically deepwater organisms and are rarely found intertidally; in addition, *T. tenuissima* has not been recorded north of Carmel Bay, while *C. gracilior* has been recorded both north and south of the study area. *Caprella uniforma* and *C. pilipalma* are intertidal species which have not been recorded north of Pacific Grove, California. *Metacaprella anomala* is an intertidal species which is occasionally found in deep water and has been recorded north and south of the study area.

Table 3 lists the caprellid species and the coastal habitat types in which the specimens were collected. The nineteen collecting sites were classified as outer coast, protected outer coast, bay and wharf piling, using the system of Ricketts and Calvin (1968) and nearshore benthos (Figs. 1 and 2). The bay habitat was divided into two sub-types: (1) those exposed at low tide and (2) those subtidal. Those exposed at low tide included mudflats, sandflats, and jetties, while subtidal

Table 3. Distribution data for the Caprellidae of the northern California coast. Numbers indicate specimens collected.

	Oregon border	Freshwater rocks	Cape Mendocino	Pt. St. George	Battery Pt.	False Klamath Cove	Abalone Beach	Trinidad Bay	Cimberg's Rock	Shelter Cove	Fort Bragg (1)	Fort Bragg (2)	Samoa Boat ramp	Coast Guard jetty	Buhne Pt.	Elk River slough	Artificial reef	Field's Landing	P. G. & E.
Habitat type	OC →	→	→	→	→ POC	→	→	→	→	→	→	→	→	→	→	→	→ WP	BAY	(1) →	→	→ (2)	→	→	→	→
# of samplings	1	1	1	1	1	1	4	8	3	1	1	1	4	1	1	1	9	2	1
Species																			
Perotripus brevis								3											
Caprella brevirostris											1	10							
C. greenleyi							2		1										
Cercops compactus					1	2	2			1									
Tritella laevis				9	56		33			13		8							
Caprella verrucosa				1	4	5		3	29			4							
C. alaskana								2					1						
C. natalensis					4			1	6		11	28			55				
C. incisa				6	31	1		6			3	389			77		14		
Deutella californica							1	12				1	23	6		20	152	61	
Caprella laeviuscula							5	183					64			2	1,825	16	
C. californica							1	2					9			3	436	111	
Metacaprella kennerlyi		2						13	3		9		1				1		
Tritella pilimana	421	19	1			9		73	3				57	5		11	1,094	2	
Caprella ferrea		7						42			1	1	5						
C. pustulata	19	6					4						1			5			
C. equilibra																	257	1	42
C. acanthogaster humboldtiensis																		126	

locations were floating docks, an artificial reef in South Humboldt Bay, and floating debris.

There were three outer coastal (OC) habitat sites, nine protected outer coastal (POC) habitat sites, one wharf piling (WP) habitat site, and seven bay (BAY) habitat sites. An attempt was made to correlate the distribution of the listed caprellid species with the type of coastal habitat in which they were found.

The outer coast was characterized by four species and all these were present on the protected outer coast, which possessed the most diverse caprellid fauna of all the coastal habitat types. Sixteen species of caprellids characterized this habitat.

The wharf piling habitat was characterized by seven species, and appears to be quite similar in its species composition to that of the bay habitat in which eleven species were found. *Tritella pilimana* was the most cosmopolitan species found throughout the study area. *Caprella equilibra* and *C. acanthogaster humboldtiensis* were found only in subtidal situations. *Caprella equilibra* was the only species present in the outflow canal of the Pacific Gas and Electric Company Nuclear Power Plant, where the water temperature was 21C as compared to the normal temperature range of Humboldt Bay of 9–13C.

It is suspected that the distribution of the listed caprellid species within the study area is influenced by the amount of wave action in the specific habitat type. Keith (1971) speculated that temperature and the amount of wave action are the primary factors affecting caprellid distributions. Other investigations have shown that temperature and salinity are the primary factors affecting the distribution of these organisms (McCain, 1968; Laubitz, 1970). Another potential factor is the duration of exposure at low tide.

The nearshore benthos off Humboldt Bay yielded *Caprella mendax, Metacaprella kennerlyi* and a third species of questionable identification. The questionable species is thought to be *Caprella ciliata* G. O. Sars (1882); a single specimen was obtained in a rock trawl at 100 m. This caprellid has previously been recorded in deep water off Alaska. Its poor condition made positive identification impossible. Laubitz (pers. comm.) has agreed that this is probably *C. ciliata*. Future collections within the study area should yield an even more diverse caprellid fauna than that reported here.

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